

The life cycle of *Pteroclava krempfi* (Cnidaria, Hydrozoa, Cladocorynidae), with notes on *Asyncoryne philippina* (Asyncorynidae)*

F. BOERO¹, J. BOUILLON² and N. GRAVIER-BONNET³

¹Dipartimento di Biologia, Stazione di Biologia Marina, Università di Lecce, 73100 Lecce, Italy.

²Laboratoire de Zoologie, Université Libre de Bruxelles, Ave F. D. Roosevelt 50, 1050 Bruxelles, Belgium.

³Laboratoire d'Ecophysiologie, Faculté des Sciences, Université de La Réunion, 15 Av. R. Cassin, 97489 St Denis Cédex, France (Ile de la Réunion).

SUMMARY: The adult medusa of *Pteroclava krempfi* is described for the first time. Morphology of both newly liberated medusa and hydroid is defined and compared to former descriptions. A distinctive character of the medusa is the presence of telotrichous macrobasic euryteles in exumbrellar pouches above the two perradial tentaculate tentacular bulbs, and the absence of exumbrellar pouches above the two perradial tentaculate tentacular bulbs. The hydroid of the nominal species *Zancloidea philippina* is reported for the first time since its initial description, confirming its referral to the genus *Asyncoryne*. The definition of the family Cladocorynidae is discussed and modified, with discussion of the superfamily Zancleoidea.

Key words: Cnidaria, Hydrozoa, Anthomedusae, Zancleoidea, life cycle, taxonomy, phylogeny.

RESUMEN: CICLO BIOLÓGICO DE *PTEROCLAVA KREMPFI* (CNIDARIA, HYDROZOA, CLADOCORYNIDAE), CON NOTAS SOBRE *ASYNCORYNE PHILIPPINA* (ASYNCORYNIDAE).— Se describe por primera vez la medusa adulta de *Pteroclava krempfi*. Los caracteres morfológicos de la medusa recién liberada y del hidropólipo se comparan con las descripciones previas. El carácter diferencial de la medusa es la presencia de nematocistos del tipo telotricos euriteles macrobásicos en las bolsas exumbrelares, situadas por encima de los dos bulbos tentaculares perradiales. El hidropólipo de la especie *Zancloidea philippina* se ha encontrado por primera vez desde su descripción, confirmando su adscripción al género *Asyncoryne*. Se discute y modifica la definición de la familia Cladocorynidae y de la superfamilia Zancleoidea. (Traducido por el Editor).

Palabras clave: Cnidaria, Hydrozoa, Anthomedusae, Zancleoidea, ciclo biológico, taxonomía, filogenia.

INTRODUCTION

Knowledge of life cycles of the superfamily Zancleoidea is rather scant (see BOUILLON, 1985; PETERSEN, 1990), and whole genera are known only, or mainly, from the medusa: *Ctenaria*, *Pteronema* (see MAYER, 1910), *Oonautes* (see KRAMP, 1959); or

from the polyp: *Rosalinda* (see ANTSULEVICH and STEPANJANTS, 1985), *Pteroclava* (see HIROHITO, 1988), *Asyncoryne* (here considered as identical with *Zancloidea*, see below) (see BOUILLON, 1974). Other genera are represented by forms with fixed gonophores or reduced medusae: *Millepora* (see LEWIS, 1991), *Cladocoryne* (see BOUILLON *et al.*, 1987), *Pseudosolanderia* (see BOUILLON and GRAVIER-BONNET, 1987; HIROHITO, 1988, as

*Received March 30, 1994. Accepted July 27, 1994.

Rosalinda sagamina in PETERSEN, 1990), *Halocoryne* (see PIRAINO *et al.*, 1992), *Zanclella* (see BOERO and HEWITT, 1992). The genus *Teissiera* is known from both hydroid and medusa stages (see BOUILLON, 1974, and BOUILLON and BOERO, 1987). The most widespread genus, *Zanclea*, is represented by species with both hydroid and medusa stages but, as remarked by PETERSEN (1990, p. 141), species definition "is in a state of chaos". Reconstruction of life cycles is thus much needed to complete the gaps in the available knowledge of this superfamily.

In this paper the complete life cycle of *Pteroclava krempfi* (BILLARD, 1919) (Cladocorynidae) is described, and the hydroid *Asyncoryne philippina* (HARGITT, 1924) (Asyncorynidae) is reported for the first time since its original description.

MATERIAL AND METHODS

Type material of *Clava krempfi*, Type H.L. 020 from Nha-Trang Bay, Vietnam, was examined from the collections of the Muséum National d'Histoire Naturelle of Paris.

Colonies of *Pteroclava krempfi* growing on alcyonaceans and gorgonians were collected by diving on the reefs of Laing Island and Boisa Island (Bismarck Sea), and La Réunion Island (Indian Ocean) at depths between 5 and 10 m. Newly released medusae were obtained from such colonies, and reared for a few days. Adult medusae were obtained from plankton tows at Laing Island.

Colonies of *Asyncoryne philippina* were obtained from a dredging off Sainte Suzanne, La Réunion Island, between 345 and 375 m depth, growing on gorgonians (Oceanographic Cruise n° 32 of "Marion Dufresne").

Specimens of *Zanclea* were obtained from the United Kingdom: Natural History Museum, London, nr 1964.8.7.9 (as *Gemmaria implexa*, det. W.J. REES); NHML nr 1969.12.2.103 (as *Zanclea implexa* det. F.S. RUSSELL and W.J. REES); Roscoff, France, and Naples, Italy: Institut Royal de Sciences Naturelles de Belgique nr 27838 (as *Zanclea costata* and *Zanclea sessilis*, det. J. BOUILLON); Seychelles, IRSNB nr 27838 (as *Zanclea* sp., det. J. BOUILLON).

Specimens of *Asyncoryne rnyiensis* were from: South Africa, NHML nr 22.3.6.5., co-type, and IRSNB nr 27838; Papua-New Guinea and Seychelles, IRSNB nr 27838.

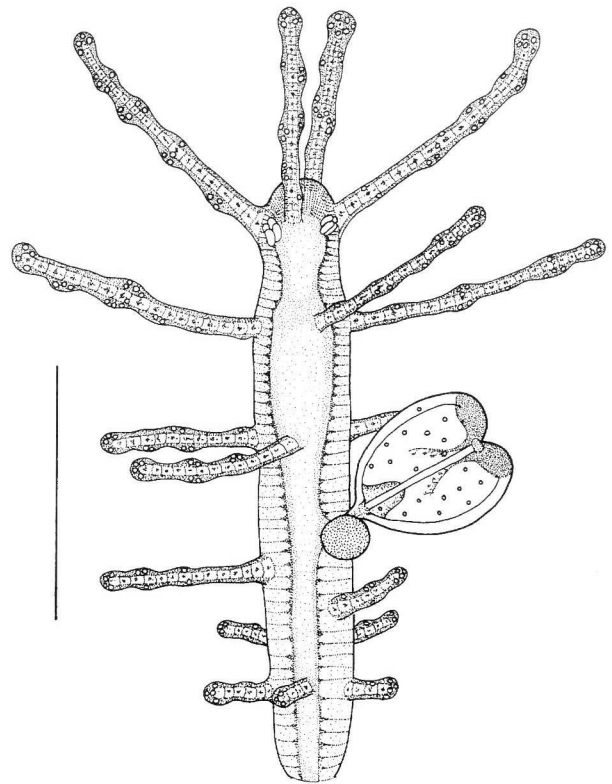


FIG. 1. – *Pteroclava krempfi*. Hydranth in optical section, from a colony growing on a soft bodied alcyonarian. Scale bar 0.5 mm.

RESULTS

Pteroclava krempfi (BILLARD, 1919)

Clava krempfi BILLARD, 1919: 187–188, Fig. 1; VAN PRAËT, 1979: 874, Fig. 3.

Pteroclava krempfi WEILL, 1931: 60–61; WEILL, 1934: 73, 74, 78, 79, 101, 111, 186, 187, 307, 356, 423–429, 433, 440, 442, 444, 446, 448, 449, 455, 641, 645, 650, 651, Figs 63, 72, 261–265; WEILL, 1936: 526, 530; RANSON, 1937: 320; LELOUP, 1937: 9; WEILL, 1937: 468, Fig. 5A; PICARD, 1957: 6; KRAMP, 1961: 444; VERVOORT, 1966: 391; BOUILLON, 1974: 134, 135, 140, 141; PETERSEN, 1979: 128; BOUILLON, 1985: 117; HIROHITO, 1988: 55–56, Fig. 17; PETERSEN, 1990: 138, Fig. 10 A, B.

? *Syncoryne crassa* PICTET, 1893: 8–9, Pl. I, Figs 3–4; HARTLAUB, 1905: 524; HARTLAUB, 1907: 112 (as *Zanclea*?); MAYER, 1910: 50; PRÉVOT, 1959: 97.

Hydroid (Figs 1, 2A, 3B, C, D)

Colonies growing on alcyonaceans and gorgonians, with perisarc-covered hydrorhizae embedded

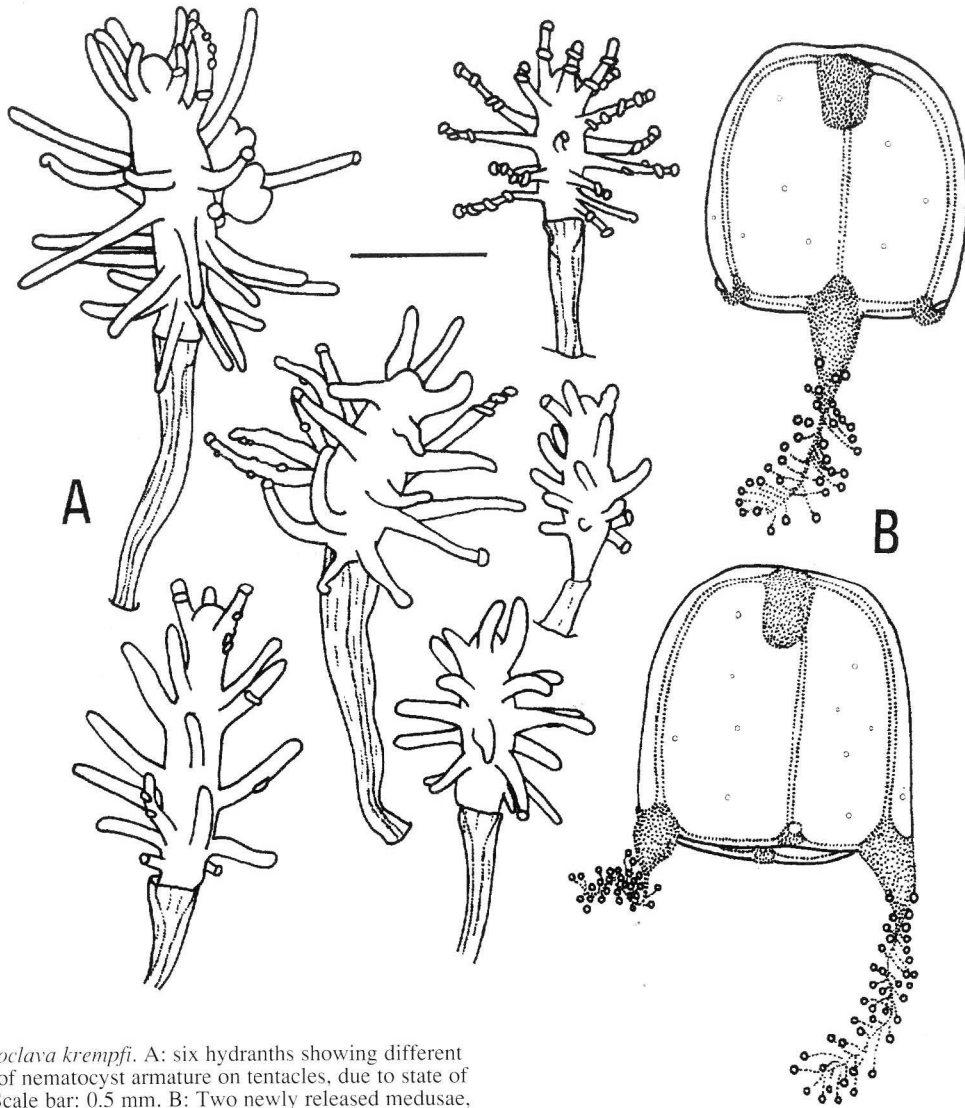


FIG. 2. — *Pteroclava krempfi*. A: six hydranths showing different stages of loss of nematocyst armature on tentacles, due to state of preservation. Scale bar: 0.5 mm. B: Two newly released medusae, bell height 0.7 mm.

in the host tissues. Hydranths about 1 mm high, emerging directly from host tissues (Fig. 1), or borne on pedicels covered by finely striated perisarc (Figs 2A, 3B, C, D), with up to 30 quasi-moniliform tentacles scattered on an elongate body. One to four patches of big nematocysts under the oral tentacles. Gonophores as medusae borne singly or in groups of up to three on short pedicels scattered in the mid region of hydranth. Nematocysts: big telotrichous macrobasic euryteles (in patches under oral tentacles), and stenoteles of two sizes mainly on tentacles (Figs. 5A, B, C, D, E).

Newly released medusa (Figs 2B, 4)

Exumbrella bell-shaped, 0.7–0.8 mm high, with thin mesogloea, four radial canals, two perradial

tentacles with big bulbs and about thirty abaxial ciliated cnidophores, two small non-tentaculate perradial bulbs with exumbrellar nematocyst pouches. Manubrium conical, shorter than half length of subumbrellar cavity. Velum present. Bulbs and manubrium white, rest of umbrella transparent. Nematocysts: big telotrichous macrobasic euryteles in exumbrellar pouches, telotrichous microbasic euryteles on exumbrella, telotrichous macrobasic euryteles in cnidophores, no stenoteles (Figs. 5A, B, C, F, G, H).

Adult medusa (Fig. 3A)

Exumbrella rounded, about 2 mm high, with thin mesogloea, four radial canals, two perradial tentacles, with big bulbs clasping the exumbrellar margin

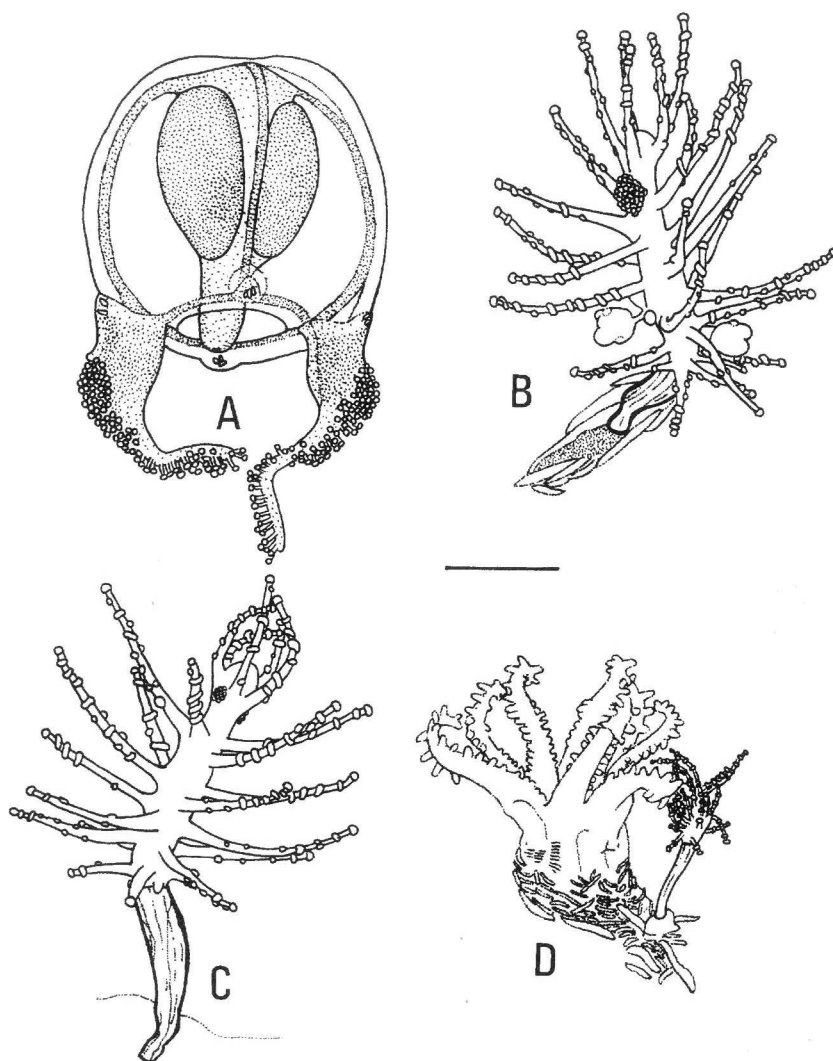


FIG. 3. – *Pteroclava kremplii*. A: adult male medusa; B, C: hydranths growing on gorgonians; D: hydranth touching a tentacle of host's polyp. Scale bar: 0.5 mm (A, B, C); 1 mm (D).

and about a hundred abaxial cnidophores. Two small, non-tentaculate perradial bulbs with nematocyst pouches. Manubrium conical, slightly extruding from velar opening, with four interradian gonads over two thirds of manubrium, leaving a free oral region (proboscis?). Nematocysts: big telotrichous macrobasic euryteles in exumbrellar pouches and at the apex of tentaculate perradial bulbs, telotrichous macrobasic euryteles in cnidophores and tentaculate tentacular bulbs (Figs. 5A, B, C, G, H).

Remarks

Hydroid:

– Tentacles

The description of hydranth tentacles of the genus *Pteroclava* is confused in the old reports.

They were variously considered as filiform, capitate, claviform, and moniliform. HIROHITO (1988) was the first to have good and abundant material of *P. kremplii* and reported the tentacles as usually moniliform, already mentioning the contradictions in the previous literature. HIROHITO rightly avoided the description of a new species from his material with moniliform tentacles, stating that earlier descriptions of the tentacles of *P. kremplii* did not allow a precise comparison (see also below). The state of preservation is the cause for discrepancies in the descriptions of tentacle structure. Our material is composed of colonies in different states of preservation. Properly anaesthetized and preserved specimens have tentacles which are moniliform distally, whereas nematocyst rings are usually not complete proximally, suggesting a cateniform structure (Fig. 3B, C). Nematocysts tend to disappear in badly preserved material. Sometimes only the distal knob

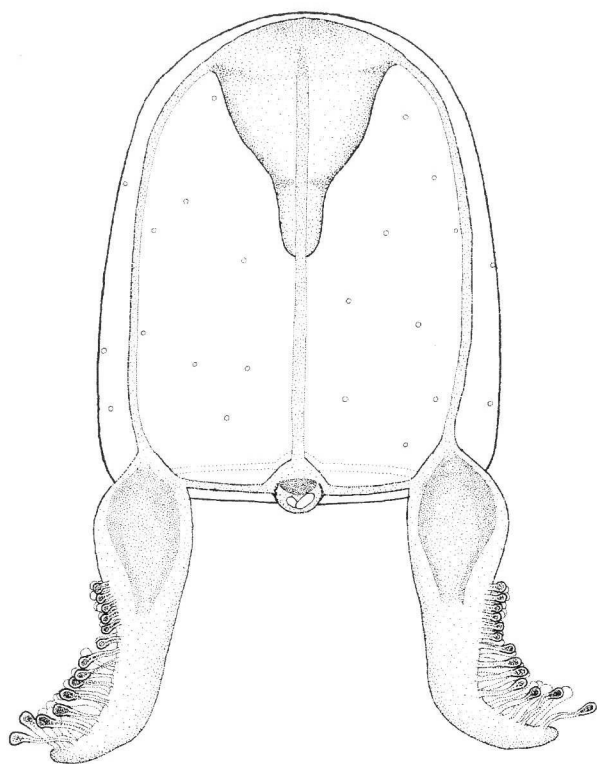


FIG. 4. – *Pteroclava krempfi*. Newly released medusa, bell height 0.7 mm.

remains, giving a capitate appearance to the tentacle, whereas, when all nematocysts are absent, the tentacles appear filiform (Fig. 2A). Such gradation of features is evident also in type material. Furthermore, some oral tentacles of type specimens mounted on slides have a semi-filiform appearance. This has been observed in other material and could be an artefact due to the state of preservation. No fresh material from the type locality was available for this study, so this feature cannot be properly evaluated. If the tentacles of specimens from the type locality prove to be semi-filiform, the material from other localities (namely Japan, Papua-New Guinea, and La Réunion Island) will differ in this feature and will need to be assigned to a species different from *Pteroclava krempfi*.

– Nematocyst patches

Badly preserved material tends to lack the typical patches of macrobasic euryteles (Fig. 2A), and sometimes only some isolated nematocysts remain. PETERSEN (1990) included *Pteroclava* in the Cladocorynidae ALLMAN, because both

Cladocoryne and *Pteroclava* share distinctive nematocyst patches of macrobasic euryteles near the oral tentacles. Patches of macrobasic euryteles have been recorded also from the hydranth body of *Eudendrium glomeratum* PICARD (see MOTZ-KOSSOWSKA, 1905, as *E. ramosum*), so this feature is not exclusive to the Cladocorynidae. However, we provisionally agree with PETERSEN's (1990) interpretation and we consider the presence of such patches in *Eudendrium* as convergent.

– Perisarc and pedicels

Depending on the host, the hydranth of *Pteroclava krempfi* emerged directly from the hosting alcyonacean (Fig. 1), or was borne on a pedicel

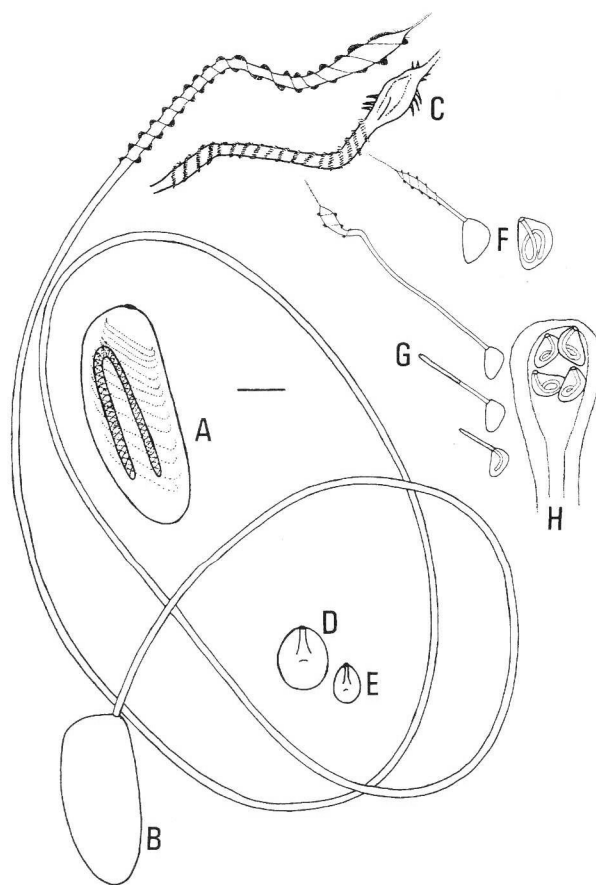


FIG. 5. – *Pteroclava krempfi*. A: undischarged telotrichous macrobasic eurytele from both hydranth patches and medusan nematocyst chambers and apex of tentaculate tentacular bulbs. B: the same, discharged. C: the same, with differently everted shaft (possibly due to compression). D, E: stenoteles of two sizes from hydroid tentacles. F: discharged and undischarged telotrichous microbasic euryteles from exumbrella of newly liberated medusa. G: three stages of discharge of telotrichous macrobasic euryteles in cnidophores of the medusa; H: optical section of a not fully developed cnidophore containing undischarged macrobasic euryteles (ciliation not shown). Scale bar: 0.01 mm.

(Figs 2A, 3B, C, D). Pedicels were longer in specimens inhabiting hosts rich in superficial spicules such as gorgonians, and less evident in fleshy alcyonaceans. The hydranth cannot retract into the pedicel but is "seated" inside it with a short basal part followed by a sharp constriction. This is very evident in type material.

– Relationship with host

Observation of living material did not allow study of the behaviour of *Pteroclava*, but some specimens fixed after careful anaesthetization (Fig. 3D) showed that the hydranths can actually touch the tentacles of the host. PIRAINO *et al.* (1992) and BOERO and HEWITT (1992) showed respectively that the hydroids of *Halocoryne* and *Zanclella* can have specialized relationships with their bryozoan hosts, feeding on their tentacles or sharing their food. It is possible that other epizoic hydroids feed in a similar manner. BILLARD (1919), followed by LELOUP (1937), considered *Pteroclava krempfi* to be parasitic, stating that it did not cause much damage to its host, but the nature of such a "parasitism" was not clearly stated and probably referred only to the growth of the hydrorhiza under the host tissues. Research on other Zancleoidea (i.e. *Zanclea* spp., *Halocoryne*, *Zanclella*) has shown that growth of hydrorhizae in host tissues does not itself indicate a parasitic relationship (OSMAN and HAUGNESS, 1981; RISTEDT and SCHUHMACHER, 1985; PIRAINO *et al.*, 1992; BOERO and HEWITT, 1992).

Medusa

– Exumbrellar pouches

Until the present, all zancleoid medusae were known to have four exumbrellar nematocyst pouches. The medusae of *Pteroclava* are exceptional in having just two such pouches. Contrary to other Zancleoidea (e.g. *Zanclea*, *Zanclella*, *Teissiera*, *Halocoryne*), the exumbrellar pouches contain macrobasic euryteles instead of stenoteles. The pouches are in close contact with the small perradial atentaculate bulbs, and resemble those described by PIRAINO *et al.* (1992) in the eumedusoid of *Halocoryne epizoica*. In adult medusae, big macrobasic euryteles (identical to those in the hydranth patches) are also present in the exumbrellar projection of the tentaculate tentacular bulbs, but no definite pouch has been seen to contain them. The

exumbrellar nematocyst pouches of many Zancleoidea possibly derive from the tentacular bulbs, during medusan growth either becoming detached from them, or remaining linked with them, or never becoming distinct from them. The atentaculate bulbs of *Pteroclava* are linked with the exumbrellar nematocyst pouches, whereas no distinct pouches are visible in the tentaculate bulbs despite the presence of macrobasic euryteles. The growth of the umbrella is said to occur downwards, along a gradient from the manubrium to the exumbrellar margin (PASTEELS, 1939). If directly linked with the tentacular bulbs, the exumbrellar pouches remain in their relative position to the bulbs (as occurs in the present species and in *Halocoryne*). If the link is lost, the distance between the pouches and the tentacular bulbs tends to increase as the umbrella grows (see RANSON, 1936, p. 89; and RUSSELL, 1953, p. 390).

– Tentacular bulbs and tentacles

A character that gives an easy distinction from *Zanclea* medusae is the large size of the tentaculate tentacular bulbs with respect to the umbrella, and their development over the exumbrella with projections containing big macrobasic euryteles identical to those inside the exumbrellar nematocyst pouches. The cnidophores are ciliated. Other peduncled, round structures, deprived of nematocysts, were observed on the tentacles of newly released medusae.

The tentacles extend over 3 mm in newly released medusae, so that the cnidophores are widely spaced. The intense ciliary action of the cnidophores might indicate an active feeding behaviour, but this requires further study. Young medusae are able to catch *Artemia* nauplii with their cnidophores, but this was never followed by ingestion.

– Nematocysts

The exumbrellar nematocyst pouches contain big macrobasic euryteles (and not stenoteles as in the other Zancleoidea) identical to those in the patches among the oral tentacles of the hydroid. The shaft of these nematocysts showed varied features, possibly due to the degree of discharge or to compression under the cover slip. In some instances the terminal part of the shaft was not abruptly enlarged (Fig. 5B), whereas in other cases some sort of "bulb" was observed (Fig. 5C), as figured by WEILL (1934). The

capsules of the microbasic euryteles on the exumbrella of newly released medusae (Fig. 5 F) resemble in shape the capsules of the macrobasic euryteles in the tentacular cnidophores (Fig. 5G, H). These are similar to the cnidophoral nematocysts of many zancleids.

Distinction from *Syncoryne crassa* PICTET, 1893.

The nominal species *Syncoryne crassa* was described by PICTET (1893) from Amboine Bay (Indonesia, Banda Sea), growing on the hydroid *Lytocarpus philippinus* (= *Macrorhynchia philippina*). WEILL (1934) did not cite PICTET's (1893) description of *Syncoryne crassa*, considering only BILLARD's (1919) description of *Clava kremplfi* to identify his material and to base his newly proposed genus *Pteroclava*. This was followed in subsequent treatments of *Pteroclava* (see list above). The reported differences between the nominal species *Syncoryne crassa* and *Clava kremplfi* are almost exclusive to the supporting host, the original description of PICTET (1893) being based on material more similar to the specimens studied here than to that of the description of *Clava kremplfi* by BILLARD (1919). Even though *Pteroclava kremplfi* had been recorded from different cnidarian hosts, they were invariably octocorals and no records are known from hydroids. Due to scant information about the medusa generation of PICTET's material, we tend to consider the two species as distinct due to different host preferences, but it is proposed here that *Syncoryne crassa* should be referred to the genus *Pteroclava*. It is uncertain whether they are conspecific.

Distribution of *Pteroclava kremplfi*

Type locality: Nha Trang (Viet-Nam, China Sea) (BILLARD, 1919; WEILL, 1931). Additional records: Sagami Bay (Japan, Pacific Ocean) (HIROHITO, 1988); Laing Island and Boisa Island (Papua-New Guinea, Bismarck Sea) (present paper); Ile de La Réunion (France, Indian Ocean) (present paper).

Asyncoryne philippina (HARGITT, 1924)

Zancloidea philippina HARGITT, 1924: 468; *Zancloidea philippina* HARGITT, 1924: 478–481, Pl II, Fig. 6; VERVOORT, 1966: 390; RUSSELL and REES, 1936: 130; PICARD, 1957: 1, 8.

Asyncoryne philippina, PICARD, 1957: 5, 8; BOUILLON, 1985: 118.

?*Pteronema darwinii*, PICARD, 1957: 5.

HARGITT, in the introduction of his paper on Philippine hydroids (HARGITT, 1924, p. 468) misspelled the name of *Zancloidea* as *Zancloidea*. In the original description (p. 478–481), however, the name of the genus is invariably spelt *Zancloidea*. We invoke article 24 of the International Code of Zoological Nomenclature to formally establish *Zancloidea* as the correct spelling of the name.

The present material agrees with HARGITT's description, which can be supplemented with the following observations:

Perisarc of hydrocaulus sharply ridged, delaminating at several sites along the colony, as if deposited into superimposed layers ("lamellar" *sensu* PETERSEN) (Fig. 6 A). Hydranth partly retractable into hydrocaulus. More than 40 aboral moniliform tentacles, similar to those of *Pteroclava*; five to six oral capitate tentacles. Nematocysts: stenoteles of two sizes, macrobasic euryteles (?). Proximal aboral tentacles apparently filiform in the best preserved hydranth (Fig. 6 B), but clearly moniliform in other hydranths.

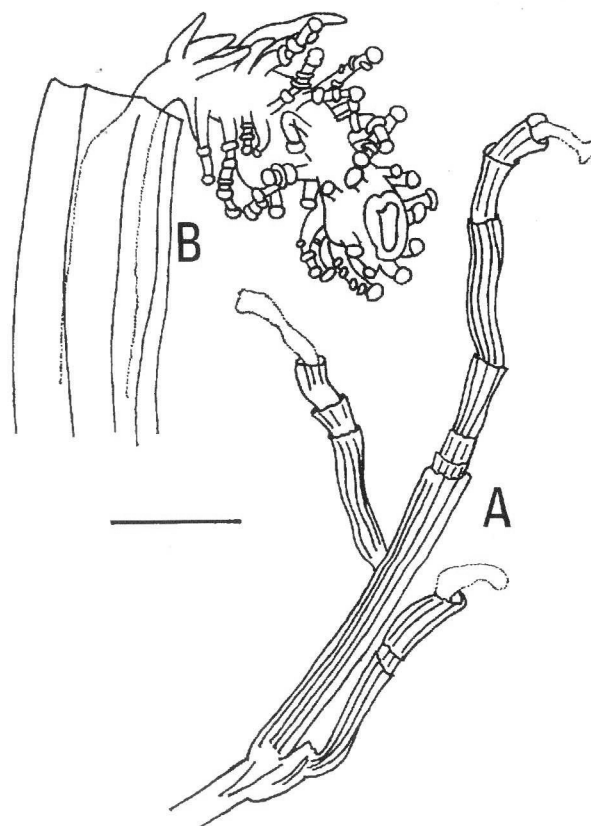


FIG. 6. — *Asyncoryne philippina*. A: stem of colony; B hydranth. Scale bar: 2 mm (A), 0.5 mm (B).

Remarks

PICARD (1957) considered *Zancloidea* as congeneric with *Asyncoryne* due to the presence of oral capitate tentacles and moniliform aboral tentacles. HARGITT (1924) stated that the medusa buds of *Zancloidea* were deprived of meridional rows of nematocysts, whereas BOUILLON (1974) reported the possibility of the existence of nematocyst pouches (with stenoteles) on the exumbrella of the newly liberated medusae of *Asyncoryne ryniensis*. PETERSEN (1990) after BOUILLON (1974, 1985) reported *Asyncoryne* medusae as having exumbrellar nematocyst pouches and used this character to include *Asyncoryne* in the Zancleidae. The presence of exumbrellar nematocyst pouches in *Asyncoryne* is confirmed by unpublished observations by GRAVIER-BONNET on *Asyncoryne ryniensis*. Both HARGITT's and our material of *A. philippina*, however, were in such a poor state of preservation that failure in observing exumbrellar nematocyst pouches does not mean that they are absent. The moniliform tentacles of *Pteroclava*, for instance, appeared filiform in badly preserved material and were described as such by many authors. Furthermore, nematocyst pouches usually derive from the apex of tentacular bulbs, so that in medusa buds they might still be in close contact with them and thus not clearly distinguishable as independent structures. Pending a detailed description of the medusae, we concur with PICARD (1957) in considering *Zancloidea* as congeneric with *Asyncoryne*. PETERSEN (1990, p. 140) reported *Asyncoryne* medusae as having four tentacles, whereas BOUILLON (1974) and GRAVIER-BONNET (unpublished) saw only two tentacles in the newly released medusae. MIGOTTO (personal communication) reared 21-day-old medusae of *Asyncoryne ryniensis* bearing developing gonads and which also presented only two perradial marginal tentacles. PICARD (1957) also proposed that *Asyncoryne philippina* could prove to be the hydroid stage of *Pteronema darwinii* HAECKEL, without providing evidence to support this statement.

DISCUSSION

Definition of the Cladocorynidae

As already stated, we provisionally accept the inclusion of both *Pteroclava* and *Cladocoryne* in the

family Cladocorynidae, as proposed by PETERSEN (1990, p. 138), whose definition of the family, however, contained several imprecisions, underlined here: "Medusae are known only from newly liberated medusae of *Pteroclava*. Two perradial tentacles with stalked cnidophores and two non-tentacular bulbs; exumbrellar nematocyst pouches absent. Hydroids with club-shaped hydranth, moniliform or capitate oral tentacles in one whorl and moniliform or modified moniliform aboral tentacles scattered or in whorls; nematocysts on body wall arranged in conspicuous rounded patches; stems simple or slightly branched rising from a creeping stolon; medusa buds carried singly or on short, branched blastostyles on lower part of hydranth; cnidome of both hydroid and medusa comprising macrobasic euryteles and stenoteles".

Exumbrellar nematocyst pouches in the newly released medusae of *Pteroclava* were described and figured by WEILL (1934, pp 405, 425, fig. 264). Their presence was also reported by BOUILLON (1985) in the diagnosis of *Pteroclava*. The present material therefore confirms that the medusae of the Cladocorynidae do have exumbrellar nematocyst pouches.

PETERSEN (1990, p. 136) stated that in *Cladocoryne* there is a "transformation from simple moniliform aboral tentacles to branched capitate tentacles", but in the definition of the family the branched capitate tentacles are treated simply as modified moniliform tentacles.

PETERSEN (1990) called *blastostyles* the peduncles on the hydranths which bore medusa buds. Blastostyles are by definition modified hydranths, and they are much different from simple peduncles. We concur with the following sentence by ALLMAN (1872, p. 34): "Notwithstanding the transition which may be thus traced between the hydranth and the blastostyle, we must carefully avoid the confounding of a true blastostyle, whose characteristic form and suppression of nutritive function show themselves *before* the appearance of the generative buds, and those pseudo-blastostyles which are caused by the extensive action of the generative buds on an ordinary hydranth".

BOUILLON *et al.* (1987) described the gonophores of *Cladocoryne haddoni* as growing from peduncles between the oral and the aboral tentacles, below the nematocyst patches. Such a disposition does not reflect the *low* position of gonophores stated by PETERSEN (1990) as being typical for the Cladocorynidae.

WEILL (1934, p. 425) did not cite stenoteles for the medusae of *Pteroclava kremppi*, and these nematocysts were not found in the present material. Euryteles and stenoteles are therefore present in the hydroid stage, whereas the cnidome of the medusa is composed solely of euryteles.

WEILL (1934, p. 425), furthermore, cited microbasic euryteles scattered on the exumbrella of the newly released medusa of *Pteroclava kremppi*, a feature confirmed by our observations. The euryteles of the Cladocorynidae are therefore both micro- and macrobasic.

The above remarks and the present description of the adult medusa of *Pteroclava* allow integration of PETERSEN's (1990) definition of the family Cladocorynidae, which is emended as follows: Cryptomedusoids or free medusae. Medusa, when present, with exumbrellar pouches containing macrobasic euryteles on non-tentaculate perradial tentacular bulbs. Tentaculate perradial tentacular bulbs with no nematocyst pouches, tentacles with cnidophores. Four interradiar gonads on manubrium. Hydroid with club-shaped hydranth, moniliform or capitate oral tentacles in one whorl and moniliform or branched capitate aboral tentacles scattered or in whorls; nematocysts on body wall arranged in conspicuous rounded patches; stems simple or slightly branched, rising from a creeping stolon; medusa buds carried singly or on short, branched pedicels on lower or middle part of hydranth; cnidome of hydroid comprising macrobasic euryteles and stenoteles; cnidome of medusa comprising micro- and macrobasic euryteles.

Affinity between the Zancleidae and the Asyncorynidae

PETERSEN (1990) included *Asyncoryne* in the Zancleidae, according to the presence of exumbrellar nematocyst pouches in the medusa, a feature confirmed by both GRAVIER-BONNET and MIGOTTO (unpublished). The presence of exumbrellar chambers and the cnidome of stenoteles and macrobasic euryteles are also shared by *Teissiera* but, currently, this is not considered as a sufficient set of characters to place this genus in the Zancleidae, due to the morphology of the hydroid. The presence of oral capitate tentacles, aboral moniliform tentacles, and lamellar perisarc enveloping both hydrorhiza and hydrocaulus are considered to be good family characters and we concur to retain the Asyncorynidae as a valid taxon (see BOUILLON, 1985, for a diagno-

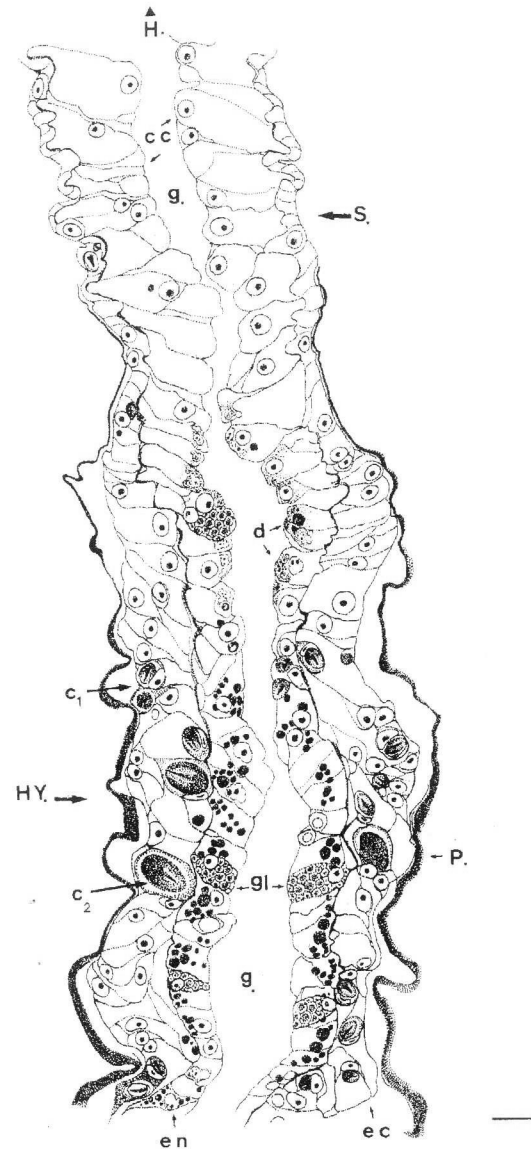


FIG. 7. — *Zanclea sessilis*. Median longitudinal histological section through the base of the hydranth (S) and the distal part of the hydrocaulus (HY). Scale bar: 0.019 mm. c_1 = stenoteles; c_2 = macrobasic euryteles; cc = chordal cells of the sphincter; d = digestive inclusions; ec = ectoderm; en = endoderm; g = gastric cavity; gl = glandular cells; H = hydranth; HY = hydrocaulus; P = perisarc; S = sphincter: limit between the digestive column of the hydranth and the hydrocaulus. Staining: hematoxylin, phloxin, light green.

sis), pending further knowledge about the morphology of their medusae. PETERSEN (1990, p. 140), furthermore, stated that "the hydroid stolons - of *Asyncoryne* - correspond to those of *Zanclea* species, being compound and enclosed in a lamellar perisarc". In our experience, *Zanclea* species have never been observed to have such distinct stolon features and PETERSEN (1990) neither cited them in the definition of the Zancleidae (p. 139) nor in the

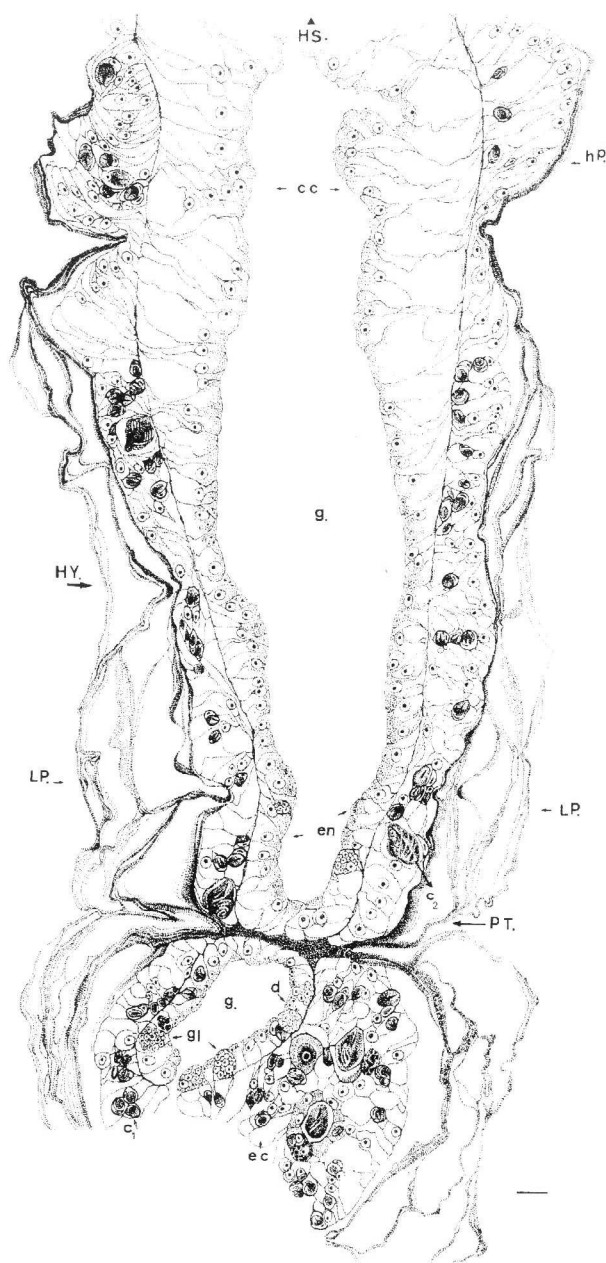


FIG. 8. – *Asyncoryne ryniensis*. Longitudinal median histological section through the proximal portion of the hydranth (HS) and the distal portion of the hydrocaulus (HY). Scale bar: 0.015 mm. hP = perisarc of the hydranth base; HS = sphincter; LP = lamellar perisarc of the hydrocaulus; PT = transversal intracoenosarcal tubular ridges of perisarc; other abbreviations as in Fig. 7.

definition of *Zanclea* (p. 141). In *Zanclea* species the perisarc is simple (Fig. 7, P), composed of the typical layers present in the majority of hydroids (see BOUILLON, 1994). However, during colony development, some hydranths might degenerate and new ones can regenerate inside the remaining old

perisarc. The new perisarc, growing up beyond the old one, might suggest a lamellar structure (see comments in RUSSELL and REES, 1936 and their figs. 5 and 7). This is a common phenomenon in hydroid colonies. In *Asyncoryne ryniensis*, on the contrary, the perisarc of both hydrocaulus and hydrorhiza is a complex inflated lamellar structure, made up of numerous distinct layers of varying thickness, irregularly and often widely separated from each other (Fig. 8, LP) (see also WARREN, 1908). Such a perisarcal system also has numerous transverse intracoenosarcal tubular connections (Fig. 8, PT), with the possible function of increasing the rigidity and strength of the perisarc tubes. Furthermore, the coenosarc of *Asyncoryne ryniensis* is locally divided into several endodermal canals (WARREN, 1908).

Remarks on the phylogeny of the superfamily Zancleoidea

PETERSEN (1990, pp. 135–137, fig. 9) provided a cladistic analysis of the Zancleoidea, opposing it to the one proposed by BOUILLON *et al.* (1987). The character state chosen by PETERSEN (1990) as common to all Zancleoidea, was the presence of stalked ectodermal cnidophores on the tentacles of the medusa (character nr 1 in the cladogram). Obviously such a character state is not applicable to the Milleporidae (which all have reduced medusae deprived of tentacles) to *Cladocoryne* (with crypto-medusoids), or to the recently described *Zanclella* (BOERO and HEWITT, 1992), or to *Halocoryne* (PIRAINO *et al.*, 1992). However, the absence of this character is the product of medusa reduction, so PETERSEN's choice could be correct.

PETERSEN (1990, p. 136) chose the hypothetical ground plan for the Zancleidae “a colonial hydroid with one whorl of moniliform oral tentacles and moniliform aboral tentacles which are scattered over the hydranth; the medusa with solid perradial tentacles and stalked cnidophores”. Having proposed an unrooted tree for the Zancleoidea, PETERSEN (1990) considered the Cladocorynidae (similar to the hypothetical ground plan of the superfamily) as the sister group to the superfamily. The Cladocorynidae are reported by PETERSEN (1990) as having medusae in which “exumbrellar nematocyst pouches - are - absent” and this led him to state (p. 136) that “the sister group of the Cladocorynidae comprises three families in which the medusae share the synapomorphic feature of exumbrellar, perradial

pouches of specialized tissue containing large stenoteles". The only difference between the Cladocorynidae and the other families of Zancleoida, as far as the exumbrellar nematocyst pouches are concerned, is that these structures contain macrobasic euryteles instead of stenoteles. Since all other Zancleoida medusae have stenoteles in the exumbrellar pouches and only the Cladocorynidae have macrobasic euryteles, this is considered to be a derived character, not shared with any known medusa. Branch 4 in PETERSEN's cladogram is incorrect due to the presence of nematocyst pouches in *Pteroclava*.

PETERSEN (1990) separated the Zancleidae from the other Zancleoida based on the presence of lamellar perisarc in the hydrorhiza. But, as remarked previously, this character is typical for *Asyncoryne* and not for *Zanclea*, and cannot be used for family distinction (besides the validity of inclusion of *Asyncoryne* in the Zancleidae, as discussed above). Branch nr 5 in PETERSEN's cladogram is also incorrect because it includes two taxa (*Asyncoryne rnyiensis* and *Zanclea* spp) that do not share the considered character. PETERSEN (1979, 1990) considered moniliform tentacles as plesiomorphic in the Capitata lineage, and this probably led him to state that *Pteroclava*, having such character, is at the base of the Zancleoida. BOERO and BOUILLON (1987) warned against considering tentacle features as a single character state for both polyps and medusae, and treated moniliform tentacles as primitive in medusae and derived in polyps.

BOERO and BOUILLON (1987) remarked that the polarization of character states and character weighting are subjective, especially in unrooted trees as those proposed by both BOUILLON *et al.* (1987) and PETERSEN (1990). In the light of the above remarks, the proper assignment of character states in PETERSEN's (1990) cladogram of the Zancleoida might call for re-consideration of the position of the Cladocorynidae. This is mainly linked to the non-separation of this family from all other Zancleoida by the absence of exumbrellar nematocyst pouches (synapomorphy nr 4 in Petersen's cladogram). The Cladocorynidae, therefore, comprises *Cladocoryne* with the most derived tentacle structure of all Capitata (the branched capitata), and *Pteroclava* with the unique apomorphy of macrobasic euryteles in the exumbrellar nematocyst pouches of the medusa. This could somehow suggest a derived position for the

Cladocorynidae, as proposed in the cladogram by BOUILLON *et al.* (1987).

Unfortunately, wide-scoped papers such as PETERSEN's (1990) revision of the Capitata inevitably contain some mistakes. The genus *Zanclea*, for instance, has a key position within the Zancleoida and its medusae have never been reported to have ocelli, but PETERSEN (1990 p. 141) reported "bulbs with abaxial ocelli" in the definition of the genus and, furthermore (p. 224), stated that "in the Zancleoida the medusae of *Zanclea* and *Teissiera* resemble each other although they differ in some characters such as the position of the ocelli which are located on the tentacle bulbs in *Zanclea* and at the aboral end of the exumbrellar nematocyst pouches in *Teissiera*". On the other hand PETERSEN (1990, p. 139), in the definition of the family, explicitly defined the Zancleidae as "without ocelli", and this is reflected in his cladogram.

We agree with PETERSEN's (1990) view that medusa reduction could have occurred independently along the same clade, and that generic distinction based only on presence or absence of free medusae could lead to the construction of paraphyletic or even polyphyletic genera. This will require a thorough reappraisal of generic taxonomy of the Hydroidomedusae, a task that PETERSEN (1979, 1990) attempted for the Capitata, although encountering many difficulties in its practical application. BRINCKMANN-VOSS (1989), KUBOTA and TAKASHIMA (1992), and PAGÈS, GILI and BOUILLON (1992), for instance, could not apply PETERSEN's (1979, 1990) classification of the Corynidae to their material. In spite of such difficulties, we are convinced that PETERSEN posed well-founded problems, even though we cannot agree with some of the solutions he proposed.

ACKNOWLEDGMENTS

The work was done with contributions from MURST (60% and 40% funds), Fonds de la Recherche Fondamentale Collective nr 29008.90, Fonds du Conseil Régional de La Réunion. P. F. S. CORNELIUS (London) and K. PETERSEN (Copenhagen) read and commented on the manuscript, without necessarily agreeing with all our positions. A. MIGOTTO (São Sebastião) allowed citation of his unpublished observations on *Asyncoryne rnyiensis*.

REFERENCES

- ALLMAN, G.O. – 1872. *A Monograph of the Gymnoblasic or Tubularian Hydroids*. Ray Society, London.
- ANTSULEVICH, A.É. and S.D. STEPANJANTS. – 1985. Novy predstavitel' redkogo roda *Rosalinda* (Hydroidea) v Dal'nevostochnykh vodakh. (A new species of a rare genus *Rosalinda* (Hydroidea) in the Far East waters). *Zool. Zhurn.*, 64(8): 1140–1147. (in Russian with English summary).
- BILLARD, A. – 1919. Note sur une espèce nouvelle d'hydroïde gymnoblasic (*Clava krempfi*), parasite d'un Alcyonaire. *Bull. Mus. natl. Hist. nat. Paris*, 25: 187–188.
- BOERO, F. and J. BOUILLON. – 1987. Inconsistent evolution and paedomorphosis among the hydroids and medusae of the Athecatae/Anthomedusae and the Thecatae/Leptomedusae (Cnidaria, Hydrozoa). In: J. BOUILLON, F. BOERO, F. CICOGLA, and P.F.S. CORNELIUS (eds.): *Modern trends in the Systematics, Ecology and Evolution of Hydroids and Hydromedusae*. Clarendon Press, Oxford, pp. 229–250.
- BOERO, F. and C. HEWITT. – 1992. A hydrozoan, *Zanclella bryozoophila* n.g., n.sp. (Zancleidae), symbiotic with a bryozoan. *Can. Journ. Zool.*, 70: 1645–1651.
- BOUILLON, J. – 1974. Description de *Teissiera milleporoides*, nouveau genre et nouvelle espèce de Zancleidae des Seychelles (Hydrozoaires: Athécates – Anthoméduses), avec une révision des hydroïdes Pteronematoidea. *Cah. Biol. mar.*, 15: 113–154.
- BOUILLON, J. – 1985. Essai de classification des Hydropolypes – Hydroméduses (Hydrozoa-Cnidaria). *Indo-Malayan Zool.*, 2(1): 29–243.
- BOUILLON, J. – 1994. Les Hydrozoaires. In: P.P. GRASSÉ and J. DOUMENC (eds.): *Traité de Zoologie* 3 (2), pp. 28–416. Masson, Paris.
- BOUILLON, J. and F. BOERO. – 1987. The life cycle of *Teissiera medusifera* (Teissieridae, Anthomedusae, Hydrozoa, Cnidaria). *Indo-Malayan Zool.*, 4(1): 1–9.
- BOUILLON, J., F. BOERO and G. SEGHERS. – 1987. Redescription of *Cladocoryne haddoni* Kirkpatrick and a proposed phylogeny of the superfamily Zancleioidea (Anthomedusae, Hydrozoa, Cnidaria). *Indo-Malayan Zool.*, 4(2): 279–292.
- BOUILLON, J. and N. GRAVIER-BONNET. – 1987. *Pseudosolanderia picardi*, nouveau genre et nouvelle espèce de Rosalindidae de la Réunion (Anthomedusae, Hydrozoa, Cnidaria). *Bull. Mus. natl. Hist. nat. Paris*, (49)(A)(4): 755–771.
- BRINCKMANN-VOSS, A. – 1989. *Sarsia cliffordi* n. sp. (Cnidaria, Hydrozoa, Anthomedusae) from British Columbia, with distribution records and evaluation of related species. *Can. J. Zool.*, 67: 685–691.
- HARGITT, C.W. – 1924. Hydroids of the Philippine Islands. *Phil. Journ. Sci.*, 24(4): 467–507.
- HARTLAUB, C. – 1905. Die Hydroiden der magelhaenischen Region und chilenischen Kuste. *Fauna Chilensis*, 3(3): 497–518.
- HARTLAUB, C. – 1907. Craspedote Medusen. I. Teil. 1. Lief. Codoniden und Cladonemiden. *Nordisches Plankton*, 6(12): 1–135.
- HIROHITO. – 1988. *The hydroids of Sagami Bay. (Part I. Athecata)*. Publications of the Biological Laboratory, Imperial Household, Tokyo.
- KRAMP, P.L. – 1959. The Hydromedusae of the Atlantic Ocean and adjacent waters. *Dana Rep.*, 46: 1–283.
- KRAMP, P.L. – 1961. Synopsis of the medusae of the world. *J. mar. biol. Ass. U. K.*, 40: 1–469.
- KUBOTA, S. and Y. TAKASHIMA. – 1992. Redescription of *Sarsia japonica* (Nagao) (Hydrozoa: Corynidae) from Hokkaido, Japan. *Publ. Seto Mar. Biol. Lab.*, 35(6): 371–381.
- LELOUP, E. – 1937. Hydropolypes et Scyphopolypes recueillis par C. Dawydoff sur les côtes de l'Indochine française. *Mém. Mus. roy. Hist. nat. Belg.*, 12: 1–73.
- LEWIS, G.B. – 1991. The ampullae and medusae of the calcareous hydrozoan *Millepora complanata*. In: R.B. WILLIAMS, P.F.S. CORNELIUS, R.G. HUGHES and E.A. ROBSON (eds.): *Coelenterate Biology: Recent Research on Cnidaria and Ctenophora*. Hydrobiologia, 216/217: 165–169.
- MAYER, A.G. – 1910. *Medusae of the world. Hydromedusae. I, II*. Carnegie Institution, Washington.
- MOTZ-KOSSOWSKA, S. – 1905. Contribution à la connaissance des hydres de la Méditerranée occidentale. I. Hydres Gymnoblasicques. *Arch. Zool. expér. gén.*, 3(4): 39–98.
- OSMAN, R.W. and J.A. HAUGNESS. – 1981. Mutualism among sessile invertebrates: a mediator of competition and predation. *Science*, 211(4484): 846–848.
- PAGÉS, F., J.M. GILI, and J. BOUILLON. – 1992. Medusae (Hydrozoa, Scyphozoa, Cubozoa) of the Benguela Current (southeastern Atlantic). *Sci. Mar.*, 56 (Suppl. 1): 1–64.
- PASTEELS, J. – 1939. Variations et gradient axial chez l'hydroméduse *Cladonema radiatum*. *Ann. Soc. roy. zool. Belg.*, 69: 311–325.
- PETERSEN, K.W. – 1979. Development of coloniality in Hydrozoa. In: G. LARWOOD, and B. ROSEN (eds.): *Biology and systematics of colonial organisms. Symposia of the Systematic Association*, 11: 105–139. Academic Press, London.
- PETERSEN, K.W. – 1990. Evolution and taxonomy in capitate hydroids and medusae. *Zool. Journ. Linn. Soc.*, 100: 101–231.
- PICARD, J. – 1957. Étude sur les hydroïdes de la superfamille Pteronematoidea. I. Généralités. *Bull. Inst. océan.*, 1106: 1–12.
- PICTET, C. – 1893. Étude sur les hydres de la Baie d'Amboine. *Rev. Suisse Zool.*, 1: 1–67.
- PIRAINO, S., J. BOUILLON, and F. BOERO. – 1992. *Halocoryne epizoica* (Cnidaria, Hydrozoa), a hydroid that 'bites'. In: J. BOUILLON, F. BOERO, F. CICOGLA, J.M. GILI, and R. HUGHES (eds.): *Aspects of hydrozoan biology*. *Sci. Mar.*, 56(2–3): 141–147.
- PRÉVOT, E. – 1959. Morphologie et évolution des structures tentaculaires chez les hydres Gymnoblasic Capitata. *Rec. Trav. Stat. mar. Endoume*, 29(17): 91–126.
- RANSON, G. – 1936. Méduses provenant des Campagnes du Prince Albert I de Monaco. *Rés. Camp. sci., Monaco*, 92: 1–245.
- RANSON, G. – 1937. Cnidactines et cnidothylacées chez les anthoméduses. *Bull. Soc. Zool. France*, 42: 318–329.
- RISTEDT, H., and H. SCHUHMACHER. – 1985. The bryozoan *Rhynchozoon larreyi* (Audouin, 1826) – a successful competitor in coral reef communities of the Red Sea. *P. S. Z. N. I: Mar. Ecol.*, 6(2): 167–179.
- RUSSELL, F.S. – 1953. *The medusae of the British Isles. Anthomedusae, Leptomedusae, Limnomedusae, Trachymedusae and Narcomedusae*. Cambridge University Press, London.
- RUSSELL, F.S. and W.J. REES. – 1936. On rearing the hydroid *Zanclea implexa* and its medusa *Zanclea gemmosa* with a review of the genus *Zanclea*. *Journ. mar. biol. Ass. U. K.*, 21(1): 107–129.
- VAN PRAËT, M. – 1979. Les types de polypes d'Hydres conservés au Muséum National d'Histoire Naturelle de Paris. *Bull. Mus. natl. Hist. nat. Paris*, 4e série, 1, section A(4): 871–940.
- VERVOORT, W. – 1966. Skeletal structure in the Solanderiidae and its bearing on hydroid classification. In: W.J. REES (ed.): *The Cnidaria and their evolution. Symposia of the Zoological Society of London*, 16: 372–396.
- WARREN, E. – 1908. On a collection of hydroids, mostly from the Natal coast. *Ann. Natal Mus.*, 5: 269–355.
- WEILL, R. – 1931. Le genre *Pteroclava* n. gen., l'interprétation systématique des Pteronemidae (Hydres) et la valeur taxonomique du cnidome. *Compt. rend. hebdom. Séanc. Acad. Sci. Paris*, 192(2): 60–62.
- WEILL, R. – 1934. Contribution à l'étude des Cnidaire et de leurs nématocystes. I. Recherches sur les nématocystes. Morphologie – Physiologie – Développement. *Trav. Stat. zool. Wimeux*, 10: 1–347.
- WEILL, R. – 1936. Au sujet de la définition et de la validité du genre *Güntherella* Weill 1934. *Bull. Soc. Zool. France*, 61: 526–532.
- WEILL, R. – 1937. Contribution à l'étude des Pteronemidae (Hydrozoaires). Le cnidome de *Cladocoryne floccosa* Rotch et son interprétation (d'après les documents laissés par feu M. Philbert). *Bull. Inst. océanogr.*, 719: 1–11.

Scient. ed.: J.M. Gili.